

Esgueiria futabensis sp. nov., a new angiosperm flower from the Upper Cretaceous (lower Coniacian) of northeastern Honshu, Japan

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Received 12 December 1998, Revised manuscript accepted 12 March 1999

Abstract. Bulk sieving of samples from the Ashizawa Formation, Futaba Group (lower Coniacian) of northeastern Honshu, Japan, has yielded a well-preserved plant mesofossil assemblage comparable to those recently described from eastern North America, Europe and central Asia. The most distinctive component of the assemblage is a new species of the genus *Esgueiria* (*Esgueiria futabensis* sp. nov.), a fossil flower known previously only from the Upper Cretaceous (Campanian–Maastrichtian) of Portugal. A possible additional species of the genus has also been recovered from a second mesofossil assemblage in the Tamayama Formation (lower Santonian). The occurrence of *Esgueiria* in Europe and eastern Asia during the Late Cretaceous indicates that despite the vegetational differences between these areas inferred from fossil pollen, some elements were widespread across middle paleolatitudes, presaging the strong floristic similarities among mid- and high latitude regions of the Northern Hemisphere during the early Tertiary.

Key words : Angiosperm flower, Ashizawa Formation, Coniacian, *Esgueiria futabensis* sp. nov., Santonian, Tamayama Formation

Introduction

Studies of the early fossil history of flowering plants (angiosperms) have been revolutionized over the last 15 years by the discovery of abundant, small, well-preserved and systematically informative fossil flowers in assemblages of Cretaceous plant mesofossils from Europe and eastern North America (e.g., Friis and Skarby, 1982; Friis, 1983; Knobloch and Mai, 1984; Friis *et al.*, 1994; Crane *et al.*, 1994). These specimens have yielded important information relating to the early diversification of many lineages of extant angiosperms and the evolution of their pollination and dispersal biology (e.g., Crane *et al.*, 1995). Only recently have similar mesofossil assemblages been recognized in central Asia (Frumina *et al.*, 1995; Frumin and Friis, 1996, 1999), and we now report that they also occur in eastern Asia. In this paper we describe the most characteristic of several fossil flowers in newly discovered plant mesofossil assemblages from the Futaba Group (lower Coniacian–lower Santonian) of Northeast Japan.

Materials and methods

Plant fossils were isolated from two sets of bulk samples collected at two different levels in the Futaba Group exposed in Fukushima Prefecture, northeastern Honshu, Japan. The fossils are small, three-dimensional and charcoalfied or lignitized mesofossils. The Kamikitaba plant mesofossil assemblage (sample F16) was isolated from a poorly sorted, carbonaceous, black, sandy siltstone collected along a tributary of the Kitaba River in Kamikitaba, Hirono-machi (Study Route B of Ando *et al.*, 1995; 37°12'N, 140°57'E). These samples were from the Asamigawa Member of the Ashizawa Formation, which is interpreted as alluvial fan sediments (Ando, 1997). The Kohisa plant mesofossil assemblage (sample F11), comprised a poorly sorted, beige, sandy siltstone with scattered carbonaceous flecks. It was collected along the Kohisa River, Kohisa, Ouhisa-machi northeast of Iwaki City (Study Route N of Ando *et al.*, 1995; 37°10'N, 140°57'E). These samples were from the middle part of the Tamayama Formation, which is interpreted as braided river flood plain sediments with lagoonal facies in the uppermost part (Ando, 1997).

The Futaba Group comprises fluvial to shallow marine

sediments in the southern Abukuma Belt of Northeast Japan (Ando et al., 1995). The Ashizawa Formation is the lowermost formation in the Futaba Group, and is overlain by the Kasamatsu Formation, which itself is overlain by the Tamayama Formation. Based on the occurrence of lower Coniacian ammonites and inoceramids in the middle of the Ashizawa Formation, and a lower Santonian inoceramid (*Inoceramus amakusensis*) in the upper part of the Tamayama Formation, the Futaba Group is thought to range in age from early Coniacian to early Santonian. The age of the plant-bearing sediments in the Asamigawa Member is probably early Coniacian (ca. 89 million years before present; Gradstein et al., 1995), whereas the age of the plant-bearing sediments in the Tamayama Formation is probably early Santonian (ca. 85 million years before present; Gradstein et al., 1995).

Bulk samples of ca. 500 kg of carbonaceous, black, poorly sorted sandy siltstone were dried in the laboratory, disaggregated in water and sieved through a 0.3 mm mesh. Recovered carbonaceous debris was then cleaned in hydrofluoric and hydrochloric acids, thoroughly rinsed in water, and dried in air. Individual specimens selected for scanning electron microscopy were mounted on scanning electron microscope stubs, sputter coated with platinum-palladium and examined in a Hitachi S-800 field emission scanning electron microscope. All specimens are deposited in the paleobotanical collections of the Field Museum of Natural History, Chicago (PP).

Systematic description

Class Magnoliopsida (angiosperms)

Genus *Esgueiria* Friis, Pedersen and Crane, 1992

The genus was established by Friis, Pedersen and Crane (1992) based on material from two localities of Campanian-Maastrichtian age in the northern part of the Western Portuguese Basin, Beira Litoral, Portugal. Two species were distinguished: *Esgueiria adenocarpa* from the Esgueira locality (the type species), and *Esgueiria miraensis* from the Mira locality.

Esgueiria futabensis sp. nov.

Figures 1-1—1-8, 2-1, 2-2, 2-4, 2-5

Material.— PP45389 (holotype). Other specimens; PP 45390–PP45417.

Type Locality and Horizon.—Kamikitaba plant mesofossil assemblage (sample F16), along a tributary of the Kitaba River in Kamikitaba, Hirono-machi, (Study Route B of Ando et al. 1995; 37°12'N, 140°57'E).

Etymology.—Named after the Futaba Group, the geological unit from which the specimens were recovered.

Specific Diagnosis.—Ovary and fruit narrowly elongate, rounded at the base. Peltate (glandular) trichomes on the base of the styles, and also in rows, often of ten or more, on the hypanthium. Simple trichomes densely spaced on the surface of the ovary, calyx and styles. Prominent receptacular mounds present between the stamens and the perianth.

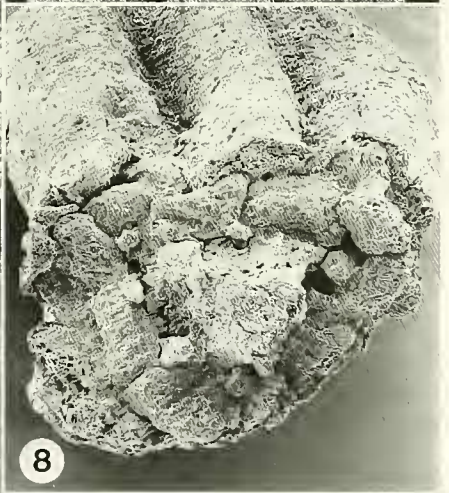
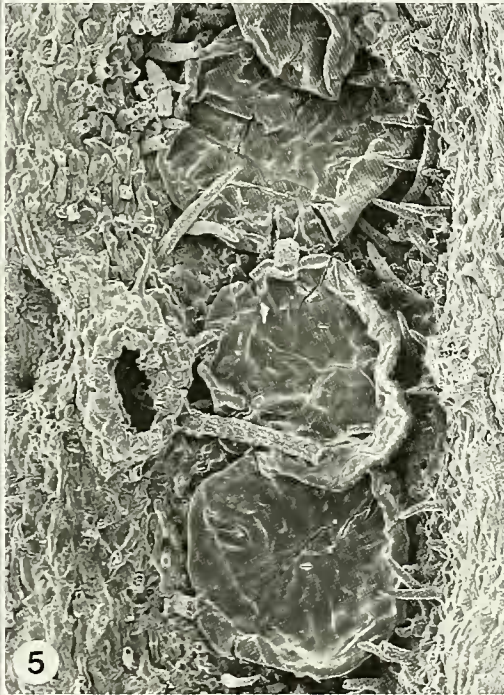
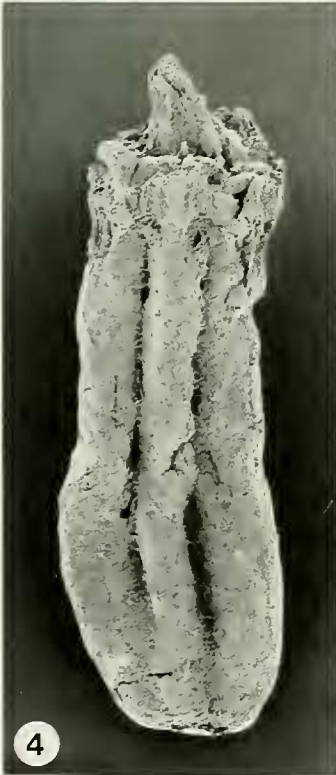
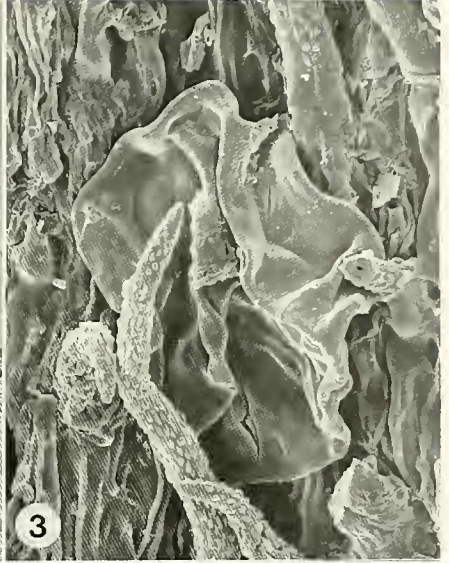
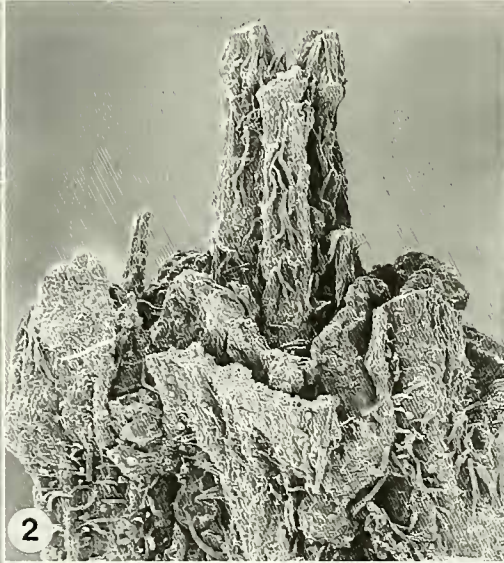
Dimensions.—All specimens lacking a well-preserved corolla: length of ovary: (1.85–) 2.76 (–3.3) mm; breadth of ovary: (0.7–) 1.12 (–1.5) mm; length of sepals: unknown; breadth of sepals: (0.3–) 3.62 (–0.4) mm: 25 specimens measured. Pollen not identified.

Description and Remarks.—The species is known from 29 complete or fragmentary flowers from the Kamikitaba assemblage preserved mainly as charcoallified specimens. Similar material from the Kohisa assemblage is not referred to *E. futabensis*, and probably represents a different species of *Esgueiria* (see below). Many of the specimens are broken or abraded fragments of the inferior ovary, but almost all show either the distinctive peltate glands, or the remains of the glands and their secretion in one or more longitudinal grooves in the ovary wall. None of the specimens is a bud and most of the material probably represents mature fruits with a partially persistent perianth and androecium. None of the specimens has yielded information on inflorescence structure, anthers, pollen or ovules.

Flower: Flowers are epigynous (Figure 1-1) and the calyx is visible in most specimens. Remains of filament and styles bases are also commonly preserved. Unequivocal remains of the petals are rarely present. None of the specimens have a pedicel or prophyll preserved.

Perianth: The calyx consists of five free sepals (Figure 1-2). In all specimens the calyx lobes are broken and their shape cannot be established reliably (Figures 1-2, 1-6, 2-5).

→ **Figure 1.** *Esgueiria futabensis* sp. nov., Kamikitaba assemblage, Asamigawa Member, Ashizawa Formation (lower Coniacian), Futaba Group, Fukushima Prefecture, northeastern Honshu, Japan. **1.** Holotype, lateral view of well-preserved epigynous flower showing peltate and simple trichomes on the ovary wall, note remains of sepals and three styles at flower apex, as well as the protruding hemispherical glands in the outer tissues of the ovary wall, PP45389, ×35. **2.** Holotype, apex of flower showing sepals, possible remains of corolla, receptacular mounds, stamen filaments and three styles, PP45389, ×73. **3.** Holotype, detail of small, peltate, trichome from base of style, note also thick wall of broken trichome, PP45389, ×930. **4.** Lateral view of abraded specimen showing ovary with longitudinal ribs denuded of trichomes, note remains of sepals and stout style base at the apex of the flower, PP45403, ×35. **5.** Holotype, detail of peltate and simple trichomes from ovary wall, note also the opening of a hemispherical gland in the ovary wall, PP45389, ×100. **6.** Detail of apical portion of specimen in Figure 1-4 showing sepals, receptacular mounds, filament bases and stout base of style, PP45403, ×72. **7.** Holotype, detail of simple trichome from ovary wall, note verrucate surface, PP45389, ×920. **8.** Detail of apex of flower in Figure 1-4 showing remains of sepals, ten prominent receptacular mounds, eight (possibly nine) filament bases and stout base of style, PP45403, ×72.



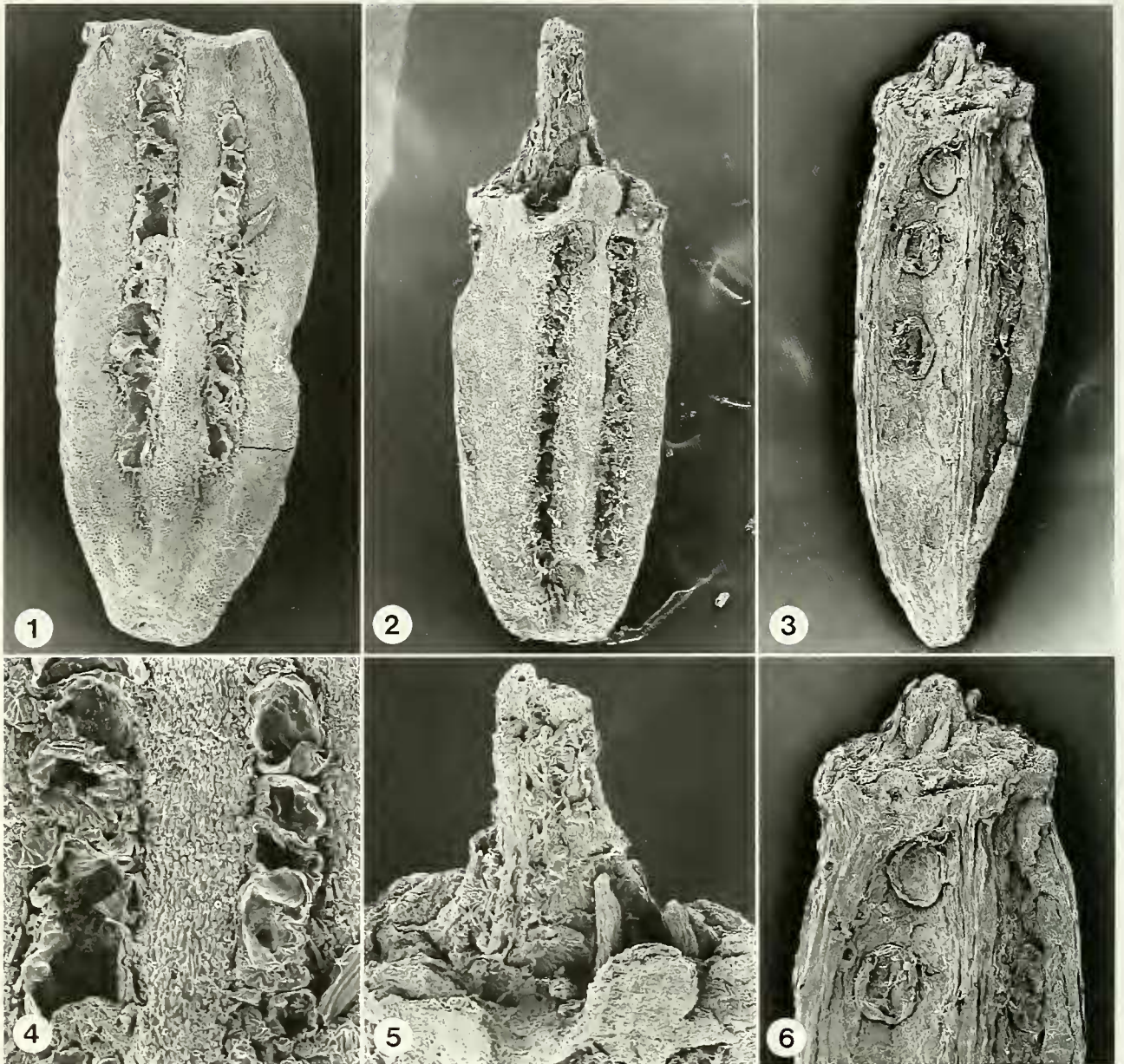


Figure 2. *Esgueiria futabensis* sp. nov. and *Esgueiria* sp., Futaba Group, Fukushima Prefecture, northeastern Honshu, Japan. 1, 2, 4, 5, *Esgueiria futabensis* sp. nov., Kamikitaba assemblage, Asamigawa Member, Ashizawa Formation (lower Coniacian). 3, 6, *Esgueiria* sp., Kohisa assemblage, middle part of the Tamayama Formation (lower Santonian). 1. Lateral view of abraded specimen showing numerous peltate trichomes in two grooves in the ovary wall, PP45391, $\times 32$. 2. Lateral view of abraded specimen showing remains of peltate trichomes in two grooves in the ovary wall, note remains of sepals and stout base of style at the floral apex, PP45393, $\times 30$. 3. Lateral view of compressed specimen showing three prominent peltate trichomes on the ovary wall, note that the peltate trichomes are larger and fewer than in *E. futabensis*, PP45419, $\times 17$. 4. Detail of specimen in Figure 2-1 showing remains of peltate trichomes and unabraded portion of ovary wall, PP45391, $\times 90$. 5. Apex of specimen in Figure 2-2 showing sepals, bases of two filaments and stout base of style, PP45393, $\times 67$. 6. Apex of specimen in Figure 2-3 showing stamen filament surrounding stout base of style, note remains of receptacular mounds between the sepals and stamen bases, PP45419, $\times 27$.

However, there are sufficient specimens in which parts of the calyx are preserved to infer that it was persistent through fruit development. The corolla is not clearly visible in any of the specimens, although a few show fragments of tissue that may represent the bases of petals. The rare presence of the corolla in more than 1,000 specimens of *E. adenocarpa* led to the conclusion that the corolla was probably caducous (Friis *et al.*, 1992), and this may also have been the case in *E. futabensis*.

Receptacular mounds: Most specimens show prominent, more or less ellipsoidal mounds of tissue, ca. 0.2 mm broad and ca. 0.1 mm deep, on the receptacle between the filament bases and the calyx (Figures 1-6, 1-8). In one specimen there are ten mounds that alternate with the stamen bases (Figure 1-8). The nature of these mounds is uncertain, but judging from their position and swollen structure (Figures 1-2, 1-6) it is possible that they are nectary lobes. A possible nectary was observed in *E. adenocarpa*, but in the more usual position for a disc nectary, between the stamens and the style bases (Friis *et al.*, 1992). In *E. futabensis* it is clear that the receptacular mounds are outside the androecium between the sepals and the stamens (Figure 1-8).

Androecium: None of the specimens has a complete stamen preserved and we have been unable to detect pollen on any of the flowers. However, the position of the stamen filaments indicates stamens were both opposite to, and alternate with, the sepals (Figure 1-8). Based on this pattern an androecium of ten stamens would be inferred. However, the best preserved androecium (Figure 1-8) shows the remains of only eight (or possibly nine) filaments. It is uncertain whether this indicates incomplete preservation, or whether less than ten stamens developed as in *E. adenocarpa* (Friis *et al.*, 1992). There is no clear indication that stamens were arranged in more than one whorl (Figure 1-8).

Gynoecium: The ovary is inferior and unilocular. The holotype clearly shows that there were three free styles, at least distally (Figure 1-2). Proximally, however the styles appear to have been fused into a single, stout, style base (Figures 1-6, 2-5). The ovary is narrowly elongated, more or less parallel-sided and with a rounded base (Figures 1-1, 1-4, 2-1, 2-2). The ovary wall is pleated into five longitudinal grooves that alternate with sepals, and five longitudinal ridges that are on the same radius as the sepals. The ovary wall is about 0.05 mm thick. In several specimens there are protruding hemispherical glands, ca. 0.1 mm in diameter, in the outer tissues of the ovary wall. In abraded specimens that lack the epidermis the inner layers of the ovary wall are seen to be composed of small equiaxial sclerenchyma cells ca. 0.01 mm in diameter. Lining the locule there is a inner epidermis of larger cuboidal cells.

Trichomes: Two different types of trichomes have been observed on the specimens. They are best developed and most easily observed on the surface of the ovary but also occur on the stout style base.

Simple trichomes: Simple hairs are scattered all over the ovary and other floral organs. The hairs may be up to ca. 0.2 mm long, are more or less parallel-sided for much of their length, and appear to be unicellular (Figure 1-7). At the apex they have an acute point. Broken specimens show

that the trichomes are thick-walled (Figure 1-3). The trichome wall close to the point of attachment seems to be thinner and somewhat collapsed (Figure 1-7). In well-preserved specimens the trichome wall is ornamented with distinctive elongated verrucae (Figures 1-3, 1-7).

Peltate trichomes: Peltate trichomes (inferred to have been glandular) are arranged in a single row in the grooves in the ovary wall (Figures 1-5, 2-4). The peltate trichomes never occur side-by-side. Smaller peltate trichomes also occur on the style bases (Figure 1-3). On the ovary wall the peltate trichomes are typically more or less circular, 0.12-0.18 mm in diameter, and appear to consist of a central stalk and a shieldlike head. A clear radiating structure among the cells comprising the head has not been seen. The number of peltate trichomes in a single row varies, but it is often between 10 and 20 (Figure 1-1, 2-1). Frequently, under the light microscope, the peltate trichomes appear to be embedded in a black shiny substance, which is often present even when the trichomes themselves are not clearly visible (Figure 2-2). We infer that this represents the remains of a secretion associated with the glandular trichomes. Peltate trichomes also occur on the style-bases of well-preserved specimens scattered among the simple hairs. These trichomes are generally smaller (ca. 0.06 mm in diameter) and less prominent than those on the ovary wall but are similar in structure (Figure 1-3).

Comparison

Esgueiria futabensis clearly shows the diagnostic features of the genus (Friis *et al.*, 1992). The flowers are small, epigynous and bisexual with the perianth and androecium organized on a basically pentamerous plan. There is a calyx of five free sepals and an androecium with more than five stamens. The ovary is unilocular with three styles. The indumentum consists of simple stiff hairs and the characteristic multicellular, peltate trichomes.

Esgueiria futabensis is clearly distinguished from the two other species of the genus. It differs from the type species, *E. adenocarpa*, in being generally larger: (1.85-) 2.76 (-3.3) mm rather than (1.5-) 1.88 (2.2) mm long. The shape of the ovary is also more or less parallel-sided, rather than obovate, and the base of the ovary is rounded rather than pointed (compare Figures 1-1, 1-4, 2-1, 2-2 with Friis, Pedersen and Crane, 1992, Plate 1). The peltate trichomes are smaller (0.12-0.18 mm in diameter) in *E. futabensis* than in *E. adenocarpa* (0.2-0.3 mm in diameter). Also significant is the number of peltate glands in a single groove on the ovary wall, which is often 10-20 in *E. futabensis*, compared with a maximum of five or six in *E. adenocarpa*.

The occurrence of peltate glands on the style bases (Figure 1-3) is a further difference between *E. futabensis* and *E. adenocarpa*, but a similarity with *E. miraensis*. However, compared to *E. miraensis*, *E. futabensis* is larger: length of ovary (1.85-) 2.76 (-3.3) mm compared to 0.8-0.95 mm. The ovary of *E. futabensis* is also long and narrow, rather than campanulate as in *E. miraensis*.

Other *Esgueiria* flowers are known from the Kohisa plant mesofossil assemblage, which is younger (early Santonian)

than the Kamikitaba assemblage that yielded *E. futabensis*. However, the Kohisa specimens are larger than those from Kamikitaba (length of ovary [2.75–] 3.5 [–4] mm), are more obovate in shape with a more pointed base, and also have significantly larger peltate trichomes (Figures 2–3, 2–6). These specimens may represent a fourth species of *Esgueiria*, but because only eight specimens are known (PP45418–PP45425), they are here left unassigned as *Esgueiria* sp.

Discussion

In terms of systematic affinities, *E. futabensis* does not add to previous discussions of a relationship between *Esgueiria* and the extant angiosperm family Combretaceae. However, this new species is important in several respects. It documents the occurrence of mesofossil assemblages with well-preserved angiosperm flowers in the Upper Cretaceous of Japan that are comparable in their quality of preservation to those recently described from eastern North America, Europe and central Asia. It adds a new species to the very small number of fossil angiosperm reproductive structures so far described from the Upper Cretaceous of Japan (Stopes and Fujii, 1910; Ohana and Kimura, 1987; Nishida, 1985, 1991, 1994; Nishida and Nishida 1988; Nishida et al., 1996). It also provides the first evidence of botanically informative plant fossil assemblages (other than palynofloras; Miki, 1977; Takahashi, 1988) in the Futaba Group.

The discovery of *Esgueiria futabensis* also has interesting biogeographic implications and extends substantially the range of a genus previously known only from the Campanian–Maastrichtian of Portugal. Based on pollen and spore assemblages Portugal was part of the Normapolles Province during the Late Cretaceous. Japan is generally included in the *Aquilapollenites* Province (Herngreen et al., 1996) based on the first appearance of triprojectate grains in Late Cretaceous sediments younger than those of the Futaba Group (Miki, 1977). The occurrence of *Esgueiria* in both eastern Asia and southern Europe documents that some Late Cretaceous floristic elements had very broad geographic distributions, presaging the strong floristic similarities evident at middle and high latitudes of the Northern Hemisphere during the early Tertiary.

Acknowledgments

This work was supported by Grant-in-Aids (08640891 and 09640827) from the Ministry of Education, Science, Sports and Culture of Japan to MT., and by fellowships from the Japan Society for the Promotion of Science in 1997 (S-97128) and 1998 (S-98106) to PRC. This work was also supported in part by U.S. National Science Foundation Grant EAR-9614672 to PRC. PRC is also grateful to Kagawa University for its hospitality during completion of this research.

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